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The millipede genus *Mandarinopus* Verhoeff, 1933, is a junior synonym of *Kronopolites* Attems, 1914 (Polydesmida, Paradoxosomatidae), with a revision of the species based on integrated evidence

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Abstract

The millipede genus *Mandarinopus* Verhoeff, 1933 (Sulciferini, Paradoxosomatidae), endemic to western China, currently comprises five species. Its taxonomic delimitation from *Kronopolites* Attems, 1914, remains controversial because of morphological similarity and overlapping distributions. Previous studies relying exclusively on morphological characters yielded ambiguous results. To clarify the taxonomic status of *Mandarinopus*, we conducted an integrative taxonomic study using topotypic specimens of all species of *Mandarinopus* and representative species of *Kronopolites*. Phylogenetic analyses based on four genetic markers (COI, 16S, 18S, and 28S rRNA) reveal that *Mandarinopus* is polyphyletic and deeply nested within *Kronopolites*. Notably, the type species of both genera form a strongly supported sister pair. Morphological re-examination demonstrates that the diagnostic characters previously used to distinguish the genera, specifically gonopodal features, are continuous and lack clear boundaries. Consequently, we formally propose *Mandarinopus* Verhoeff, 1933, as a junior synonym of *Kronopolites* Attems, 1914, transferring all valid *Mandarinopus* species to *Kronopolites*. Additionally, based on morphological and molecular evidence from topotypic material, we propose *Kronopolites rugosus* Golovatch, 2013, as a junior synonym of *Kronopolites corticinus* (Attems, 1936).

Key Words

China, morphology, molecular phylogeny, new combination, new synonym, Sulciferini

Introduction

The millipede genus *Mandarinopus* Verhoeff, 1933, belongs to the tribe Sulciferini in the widespread and speciose family Paradoxosomatidae and was established based on *Mandarinopus gracilipes* Verhoeff, 1933, from Baishuijiang, Gansu, western China. Verhoeff (1933) indicated that *Mandarinopus* is highly similar to the sympatric genus *Kronopolites*, with key differences including the sternal cone between the coxae of the 4th pair of legs and the shape of the gonopodal solenomere and solenophore. Attems (1937) treated this genus as a junior synonym of *Sundanina* Attems, 1914 (now belonging to the tribe Sundaninini). However, because of significant differences in gonopodal morphology, Jeekel (1968) reinstated the taxonomic status of *Mandarinopus* and suggested that *Mandarinopus* may be closely related to the genus *Oxidus*. This genus remained monotypic until Golovatch (2019) described a new species, *Mandarinopus hirsutus*, and transferred a questionable species, *Orthomorpha corticina*, and two *Kronopolites* species to *Mandarinopus*, that is, *Kronopolites semirugosus* Golovatch, 2013, and *Kronopolites rugosus* Golovatch, 2013, because of the similarity of their gonopods. Golovatch (2019) also provided new photographs of the type species based on newly collected specimens.

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Since then, *Mandarinopus* has been recognized to include five species, with the exception of the type species, all of which are from Yunnan Province. Additionally, similar to Verhoeff's proposition, Golovatch (2019) noted that *Mandarinopus* is morphologically close to *Kronopolites*, with the key difference being that the gonopodal solenomere and solenophore of the genus *Mandarinopus* are less curved and have a more complex structure. However, these diagnostic characteristics are highly subjective, complicating practical taxonomy. Furthermore, uncertainties persist at the species level. For instance, Golovatch (2020) noted the striking morphological similarity between *Mandarinopus corticinus* (Attems, 1936) and *Mandarinopus rugosus* (Golovatch, 2013), suggesting that they might be synonymous.

To clarify the generic status of *Mandarinopus* and validate its species, we examined topotypic specimens representing all five nominal species of the genus *Mandarinopus* and multiple *Kronopolites* species. By combining new morphological data with a molecular phylogeny based on publicly available and newly generated sequences, we aim to (1) test the monophyly of *Mandarinopus*, (2) re-evaluate generic-level diagnostic characters, and (3) revise the species composition of the group.

Materials and methods

Material collected and taxonomic identification

We collected specimens with tweezers and preserved them in 75% ethanol for morphological studies. We photographed live animals using a Sony A7R4A camera paired with a Sony FE 90 mm macro lens. All specimens are deposited in the National Resource Center for Chinese Materia Medica, China Academy of Chinese Medical Sciences, Beijing, China (**CMMI**). We numbered and stored all specimens using the collection date (year/month/day) plus an auto-incrementing serial number. We examined, photographed, and measured specimens with a Leica M205 MCA microscope equipped with a Leica DMC 6200 camera and LAS software (ver. 4.1, Leica, Germany). We edited all images using Photoshop CC (ver. 2020, Adobe, USA).

We follow the terminology established by Verhoeff (1933) and Golovatch (2019).

DNA extraction, sequencing, assembly, and annotation

We extracted total genomic DNA from leg tissue using the DNeasy® Blood & Tissue Kit (QIAGEN GmbH, Germany), following the manufacturer's extraction protocol. We sequenced the genomes on the Illumina NovaSeq™ platform of Annaroad Gene Technology (Beijing) Co., Ltd., China. We used GetOrganelle v1.7.7.1 (Jin et al. 2020) to obtain the mitochondrial genome and HybPiper v2.3.3 (Johnson et al. 2016) to obtain the ribosomal RNA genome. We annotated the mitochondrial genome using the MITOS web server (Bernt et al. 2013).

Genetic distance and phylogenetic analysis

We collected topotypic specimens of all five *Mandarinopus* species for this study. We also analyzed eight representative species of *Kronopolites*, including the type species *Kronopolites svenhedini*. In addition, we included representatives from six other genera within the tribe Sulciferini (*Anoplodesmus*, *Oxidus*, *Sellanucheza*, *Sichotanus*, *Tylopus*, and *Vietnamorpha*). We used *Antheromorpha festiva* (Brölemann, 1896) (tribe Orthomorphini) as the outgroup (Nguyen 2017).

We calculated the genetic distances of the COI gene among *Mandarinopus* and *Kronopolites* species using the Kimura two-parameter model in MEGA X (Kumar et al. 2018).

We conducted phylogenetic analyses based on four markers: two nuclear genes (18S and 28S rRNA) and two mitochondrial genes (16S rRNA and COI) (Figs 1, 2). We deposited the 18S, 28S, and 16S gene sequences in the European Nucleotide Archive (ENA) and the COI sequences in GenBank. We provide sample information, localities, and accession numbers in Suppl. material 1.

We performed both Maximum Likelihood (ML) and Bayesian Inference (BI) analyses using the concatenated dataset. We selected the GTR+F+I+G4 substitution model as the best-fit model based on the Bayesian Information Criterion (BIC), following the suggestion of ModelFinder (Kalyaanamoorthy et al. 2017). We constructed the ML tree using IQ-TREE 1.6.12 (Nguyen et al. 2015), with 1,000,000 ultrafast bootstrap replicates (Anisimova et al. 2011). We conducted the BI analysis using MRBAYES 3.2.6 (Ronquist et al. 2012), with 10,000,000 Markov chain Monte Carlo (MCMC) generations and sampling every 1,000 generations. We discarded the first 25% of trees as burn-in. We determined stationarity by a split frequency of less than 0.01 and computed a consensus tree from the remaining trees. We visualized the resulting phylogenies using FigTree v1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/).

Results

Molecular and phylogenetic analysis

Phylogenetic analyses based on maximum likelihood (ML) and Bayesian inference (BI) produced similar topological structures and are consistent with the overall framework established by Nguyen (2017). The length of the concatenated dataset is 2,480 base pairs (bp). Our results strongly support the monophyly of the combined *Mandarinopus* spp. and *Kronopolites* spp. clade (BS = 100%, PP = 1.00). The combined clade is resolved into three main subclades: Clade A, Clade B, and Clade C. Except for the type species, *M. gracilipes*, all other species of *Mandarinopus* form a strongly supported clade (Clade A) (BS = 100%, PP = 1.00). *M. gracilipes* is recovered as a sister to the type species of *Kronopolites*, *K. svenhedini* (BS = 93%, PP = 1.00). These two species, together with

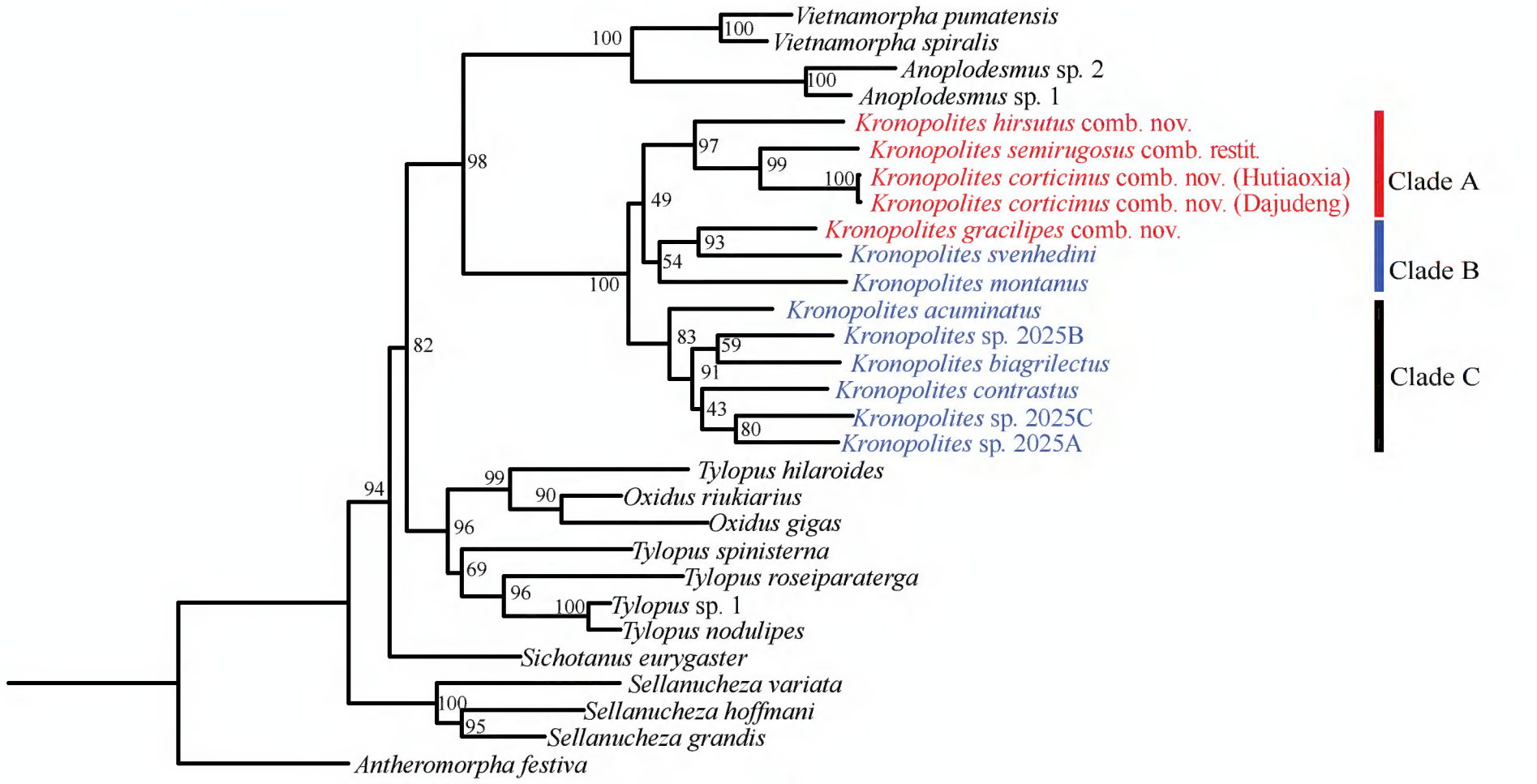

Figure 1. Phylogenetic tree inferred from the combined analysis of 16S, 18S, 28S rRNA, and COI using maximum likelihood analysis. Values above the branches represent bootstrap support. Red taxa indicate former *Mandarinopus* species, now transferred to *Kronopolites*.

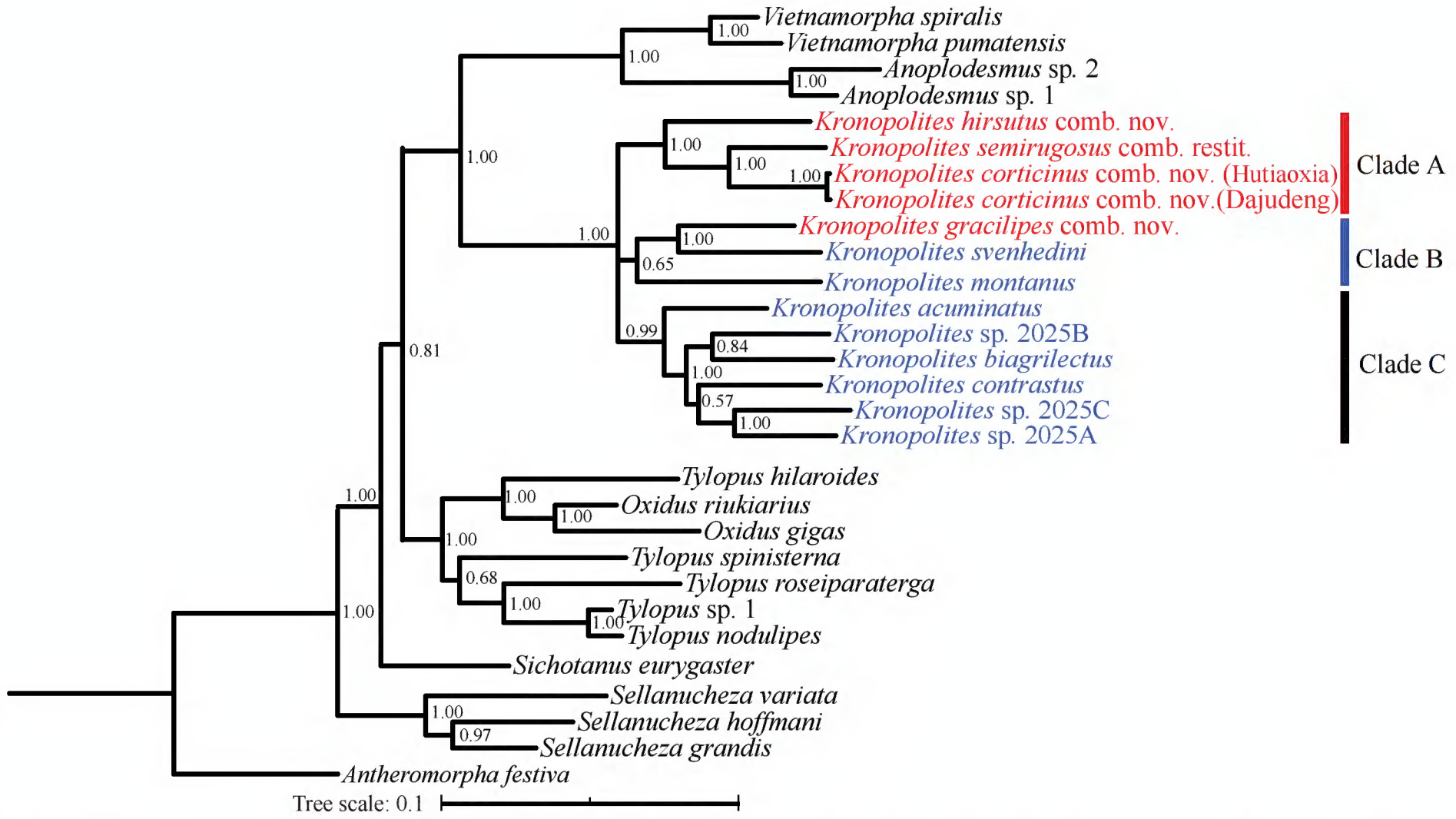

Figure 2. Phylogenetic tree inferred from the combined analysis of 16S, 18S, 28S rRNA, and COI using Bayesian inference analysis. Values above the branches represent posterior probabilities. Red taxa indicate former *Mandarinopus* species, now transferred to *Kronopolites*.

K. montanus, form Clade B. However, the monophyly of Clade B itself receives only weak support (BS = 54%, PP = 0.65). Clade C consists of the remaining *Kronopolites* species and is moderately supported (BS = 83%, PP = 0.99). The relationships among Clade A, Clade B, and Clade C remain unresolved.

Analysis of the COI gene shows that the interspecific genetic distances among *Mandarinopus* and *Kronopolites* species range from 10.99% to 18.62% (Table 1). In contrast, the intraspecific distance is 0.53% (*Kronopolites corticinus* comb. nov.), which is much lower than the interspecific distances.

Table 1. Pairwise nucleotide differences (Kimura two-parameter model) across sequence pairs between *Kronopolites* and *Mandarinopus*.

No.	Species	1	2	3	4	5	6	7	8	9	10	11
1	*Kronopolites biagrilectus*											
2	*Kronopolites contrastus*	13.65%										
3	*Kronopolites corticinus* comb. nov. (Dajudeng)	14.89%	15.43%									
4	*Kronopolites corticinus* comb. nov. (Hutiaoxia)	15.25%	15.43%	0.53%								
5	*Kronopolites gracilipes* comb. nov.	16.13%	13.12%	14.01%	14.01%							
6	*Kronopolites hirsutus* comb. nov.	16.67%	15.43%	15.07%	14.89%	14.01%						
7	*Kronopolites montanus*	15.96%	14.01%	15.78%	15.78%	13.83%	14.72%					
8	*Kronopolites semirugosus* comb. restit.	16.84%	16.31%	11.17%	10.99%	13.83%	13.30%	15.25%				
9	*Kronopolites* sp. 2025A	16.13%	15.07%	14.01%	14.01%	14.89%	15.96%	13.48%	14.89%			
10	*Kronopolites* sp. 2025B	17.38%	15.96%	18.62%	18.62%	15.78%	17.55%	14.36%	16.13%	15.25%		
11	*Kronopolites* sp. 2025C	15.25%	14.01%	14.18%	14.18%	15.07%	15.96%	16.13%	14.01%	12.59%	16.49%	
12	*Kronopolites svenhedini*	16.84%	15.43%	11.70%	11.70%	12.59%	14.36%	15.07%	13.83%	14.36%	14.54%	15.60%

Taxonomy

Family Paradoxosomatidae Daday, 1889
Subfamily Paradoxosomatinae Daday, 1889
Tribe Sulciferini Attems, 1898

Genus *Kronopolites* Attems, 1914

Kronopolites Attems, 1914: 219.

Kronopolites: Attems 1929: 272; 1931: 113; 1936: 225; 1937: 49; Verhoeff 1939: 274; Takashima 1950: 38; Takakuwa 1954: 30; Hoffman 1962: 579; 1980: 169; Jeekel 1971: 225; 1982: 243; 1988: 98; Chen et al. 2006: 252; Golovatch 2009: 121; 2013a: 12; Nguyen and Sierwald 2013: 1286; Likhitrakarn et al. 2015: 32; Golovatch 2015: 135; Golovatch 2016: 1; Golovatch 2019: 348; Golovatch and Liu 2020: 170; Golovatch and Semenyuk 2021: 479; Nguyen et al. 2025: 225.

Kansupus Verhoeff, 1933: 17; Jeekel 1971: 225; Hoffman 1980: 169; synonymized by Attems (1936: 233).

Parakansupus Verhoeff, 1939: 273; Jeekel 1971: 230; Hoffman 1980: 169; synonymized by Hoffman (1962: 579).

Mandarinopus Verhoeff, 1933: 19; Attems 1937: 159; Jeekel 1968: 72, 1988: 98; Nguyen and Sierwald 2013: 1286; Golovatch 2019: 348, 354. New synonymy.

Type species. *Kansupus svenhedini* Verhoeff, 1933 (originally it was *Strongylosoma swinhoei* Pocock, 1895, but reassigned as *K. svenhedini* due to misidentification; see Xiong et al. 2025).

Distribution. China, Vietnam, Nepal, Thailand, and Kashmir Himalaya (Xiong et al. 2025).

Revised diagnosis. Body coloration variable, ranging from pitch-black to brown, often with contrasting lighter paraterga. Coxa cylindrical, typically setose. Prefemur short, ovoid, densely setose. Femorite elongate, slender, occasionally possessing a distofemoral process (femoral thorn), though this feature may be intraspecifically variable. Postfemur distinct, typically characterized by a fork consisting of two lateral/ventral processes (processes *a* and *b*). Solenophore well-developed, varying in complexity from simple sheathing structures to complex, apically modified shapes. Solenomere flagelliform, length and curvature variable (long and coiled or shorter and less curved), sheathed by the solenophore for most of its length.

Remarks. Verhoeff (1933) established the monotypic genus *Mandarinopus* based on *Mandarinopus gracilipes*, distinguishing it from *Kronopolites svenhedini* primarily by the curvature of the gonopodal solenomere and the presence of a distofemoral process (see arrows in Fig. 5). However, our examination reveals that solenomere curvature is a variable trait that fails to diagnose the genera; for example, the solenomere in *M. semirugosus* (Fig. 9) is comparable in length and curvature to that of *Kronopolites ramosus* (figs 38–42 in Golovatch and Semenyuk 2021). Furthermore, the distofemoral process is intraspecifically unstable (e.g., *K. corticinus*; see below). Given that our phylogenetic analysis recovers *Mandarinopus* as polyphyletic and nested within *Kronopolites*, and that the morphologically diagnostic characters are unreliable, we formally propose *Mandarinopus* as a junior synonym of *Kronopolites*. Following this synonymization, the genus *Kronopolites* now encompasses 18 recognized species in total, with its composition expanded by incorporating all four valid species previously assigned to *Mandarinopus* into its taxonomic framework (Table 2).

Kronopolites gracilipes (Verhoeff, 1933), comb. nov.

Figs 3C, 4, 5

Mandarinopus gracilipes Verhoeff, 1933: 19–20, figs 10, 11. Type locality: Pei-shui-ho (= Baishuijiang River), China.

Sundanina gracilipes: Attems 1936: 223; 1937: 164, synonymized by Jeekel (1968: 72).

Mandarinopus gracilipes: Jeekel 1988: 98; Wang and Mauriès 1996: 87; Nguyen and Sierwald 2013: 1288; Golovatch 2019: 348–350, figs 6–9; Golovatch and Liu 2020: 170.

Table 2. All known *Kronopolites* species after the synonymy of *Mandarinopus*. Names are listed by year of publication and alphabetically for those from the same year.

No.	Species	Former genus	Distribution
1	*Kronopolites gracilipes* (Verhoeff, 1933) comb. nov.	*Mandarinopus*	China
2	*Kronopolites svenhedini* (Verhoeff, 1933)	*Kronopolites*	China
3	*Kronopolites corticinus* (Attems, 1936) comb. nov.	*Mandarinopus*	China
4	*Kronopolites acuminatus* Attems, 1937	*Kronopolites*	Vietnam
5	*Kronopolites formosanus* (Verhoeff, 1939)	*Kronopolites*	China
6	*Kronopolites biagrilectus* Hoffman, 1963	*Kronopolites*	China
7	*Kronopolites fuscocingulatus* Jeekel, 1982	*Kronopolites*	Thailand
8	*Kronopolites occidentalis* Golovatch, 1983	*Kronopolites*	Kashmir Himalaya
9	*Kronopolites montanus* Golovatch, 2009	*Kronopolites*	China
10	*Kronopolites semirugosus* Golovatch, 2013 comb. restit.	*Mandarinopus*	China
11	*Kronopolites davidiani* Golovatch, 2014	*Kronopolites*	China
12	*Kronopolites coriaceus* Golovatch, 2015	*Kronopolites*	Nepal
13	*Kronopolites lunatus* Likhitrakarn, Golovatch & Panha,2015	*Kronopolites*	Thailand
14	*Kronopolites hirsutus* (Golovatch, 2019) comb. nov.	*Mandarinopus*	China
15	*Kronopolites typicus* Golovatch, 2020	*Kronopolites*	China
16	*Kronopolites ramosus* Golovatch & Semenyuk, 2021	*Kronopolites*	Vietnam
17	*Kronopolites contrastus* Nguyen, Vu, Phung, Tran & Le, 2025	*Kronopolites*	Vietnam
18	*Kronopolites serratus* Nguyen, Vu, Phung, Tran & Le, 2025	*Kronopolites*	Vietnam

Figure 3. Live specimens. **A, B.** *Kronopolites corticinus* (Attems, 1936), comb. nov. from Daju Deng, Dali Bai Autonomous Prefecture, Yunnan; **C.** *K. gracilipes* (Verhoeff, 1933), comb. nov. from Qujia Village, Longnan, Gansu; **D.** *K. hirsutus* (Golovatch, 2019), comb. nov. from Dajudeng, Dali Bai Autonomous Prefecture, Yunnan. Not to scale.

Material examined. CHINA: Gansu Province: • 3 ♂♂ and 14 ♀♀ (CMMI 20250809001, 20250809018–20250808031), Wenxian County, Qujia Village (32.8852°N, 104.8263°E), asl. 940 m, 9.VIII.2025, Xuankong Jiang, Yifei Yu & Yuan Xiong leg.

Diagnosis. Differs from other species of the genus by the following combination of characters: collum and metaterga smooth; gonopod with blunt processes *a* and *b*, and a distofemoral process.

Distribution. China: Gansu (Golovatch 2019).

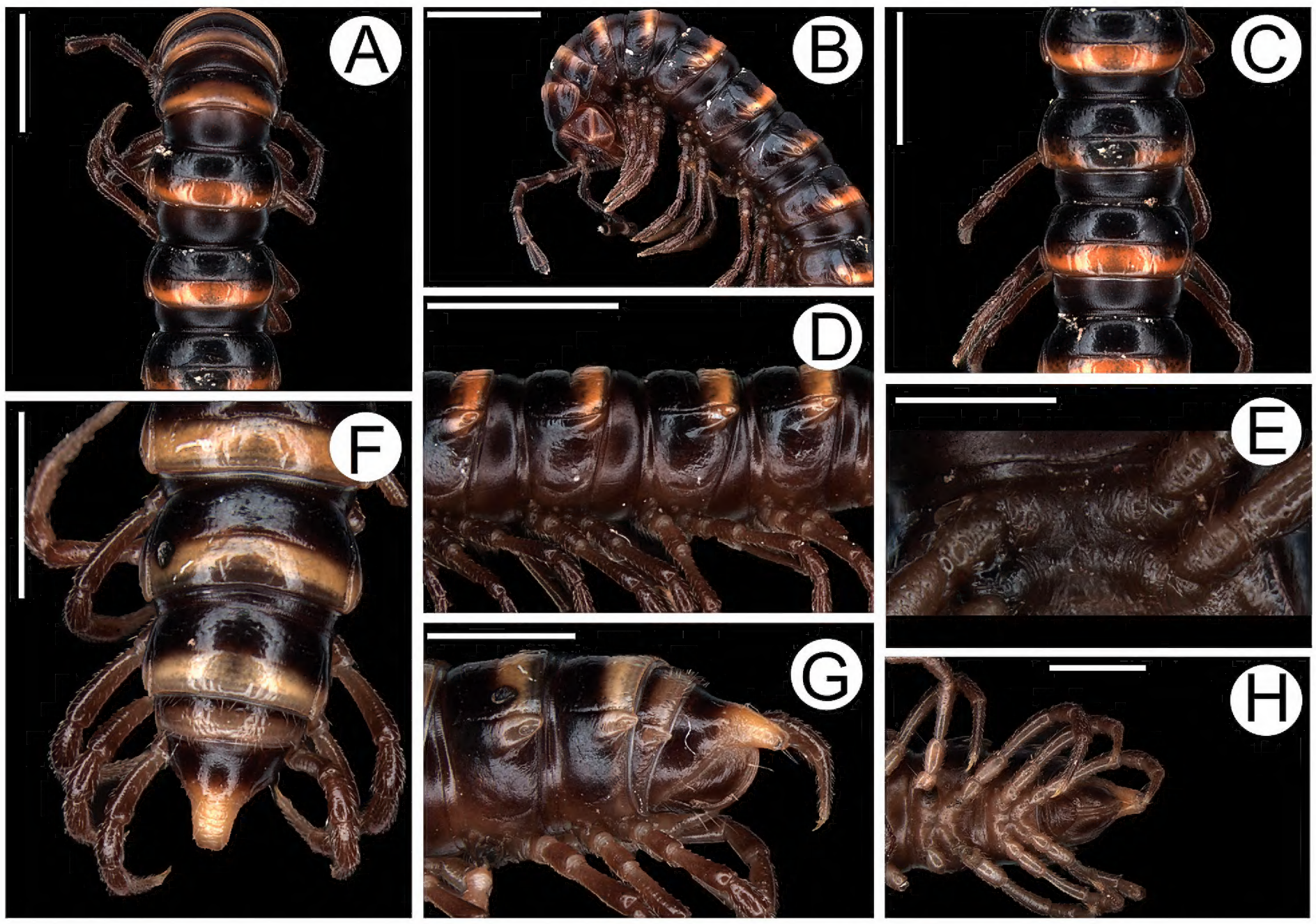

Figure 4. *Kronopolites gracilipes* (Verhoeff, 1933), comb. nov. **A.** Anterior part of body, dorsal view; **B.** Anterior part of body, lateral view; **C.** Segments 10 and 11, dorsal view; **D.** Segments 9–11, lateral view; **E.** Sternal cones between coxae 4, ventral view; **F–H.** Posterior part of body, dorsal, lateral, and ventral views, respectively. Scale bars: 5 mm (**A–D**, **F–H**); 2 mm (**E**).

Remarks. Verhoeff (1933) described a new monotypic genus and species, *Mandarinopus gracilipes*, from the Baishuijiang River, Gansu. This species has a distofemoral process (femoral thorn) (red arrow in Fig. 3) on its gonopodal femorite, referred to either as the distofemoral process (Golovatch 2019) or the sharp thorn (Attems 1937).

Kronopolites corticinus (Attems, 1936), comb. nov.

Figs 3A, B, 6, 7

Orthomorpha corticina Attems, 1936: 201, fig. 31; Attems 1937: 91, fig. 116; Jeekel 1968: 72; Wang and Mauriès 1996: 87; Nguyen and Sierwald 2013: 1288; Golovatch 2019: 354.

Mandarinopus corticinus: Golovatch 2020: 297–302, figs 7–15.; Golovatch and Liu 2020: 170.

Kronopolites rugosus Golovatch, 2013: 12; Nguyen and Sierwald 2013: 1288; Golovatch 2013b: 311; Likhitrakarn et al. 2015: 32; Golovatch 2019: 354; Nguyen et al. 2025: 224.

Mandarinopus rugosus: Golovatch 2020: 298; Golovatch and Liu 2020: 170. New synonymy.

Material examined. CHINA: Yunnan Province: • 9 ♂♂ and 3 ♀♀ (CMMI 20240528001–2024080812), Diqing Tibetan Autonomous Prefecture, Shangri-La, Hutiaoxia Scenic Area (27.2410°N, 100.1401°E), asl. 2420 m, 28.V.2024, Yifei Yu & Yuan Xiong leg.; • 6 ♂♂ and 2 ♀♀ (CMMI 20240531001–20240531008), Yulong Naxi Autonomous County, Yuzhuqingtian Scenic Area (27.0069°N, 100.2086°E), asl. 2730 m, 31.V.2024, Yifei Yu & Yuan Xiong leg.; • 13 ♂♂ and 6 ♀♀ (CMMI 20250803013–20250803031), Dali Bai Autonomous Prefecture, Jianchuan County, Laojunshan Town, Dajudeng (26.5891°N, 99.6094°E), asl. 2650 m, 3.VIII.2025, Xuankong Jiang, Yifei Yu & Yuan Xiong leg.; • 3 ♂♂ and 4 ♀♀ (CMMI 20250805137–20250805143), Yulong Naxi Autonomous County, Tuozhi Village (27.1500°N, 99.6915°E), asl. 2310 m, 5.VIII.2025, Xuankong Jiang, Yifei Yu & Yuan Xiong leg.

Diagnosis. Differs from other species of the genus by the following combination of characters: coloration dark brown to brown with contrasting yellowish paraterga; collum and following metaterga rugose; sternal cones between ♂ coxae 4 fully separated; gonopods with basal process of solenophore much larger than a slender, finger-shaped, apical process (Golovatch 2019).

Distribution. China: Yunnan (Golovatch 2019).

Remarks. *Orthomorpha corticina* Attems, 1936 was originally described from specimens collected at an unspecified locality in Yunnan Province, China. Long treated as *incertae sedis* within the tribe Sulciferini (Jeekel 1968; Nguyen and Sierwald 2013), the species was redescribed based on newly collected specimens from

Figure 5. *Kronopolites gracilipes* (Verhoeff, 1933), comb. nov., left gonopod. **A.** Ventral view; **B.** Mesal view; **C.** Lateral view. Red arrows indicate the distofemoral process. Scale bar: 2 mm.

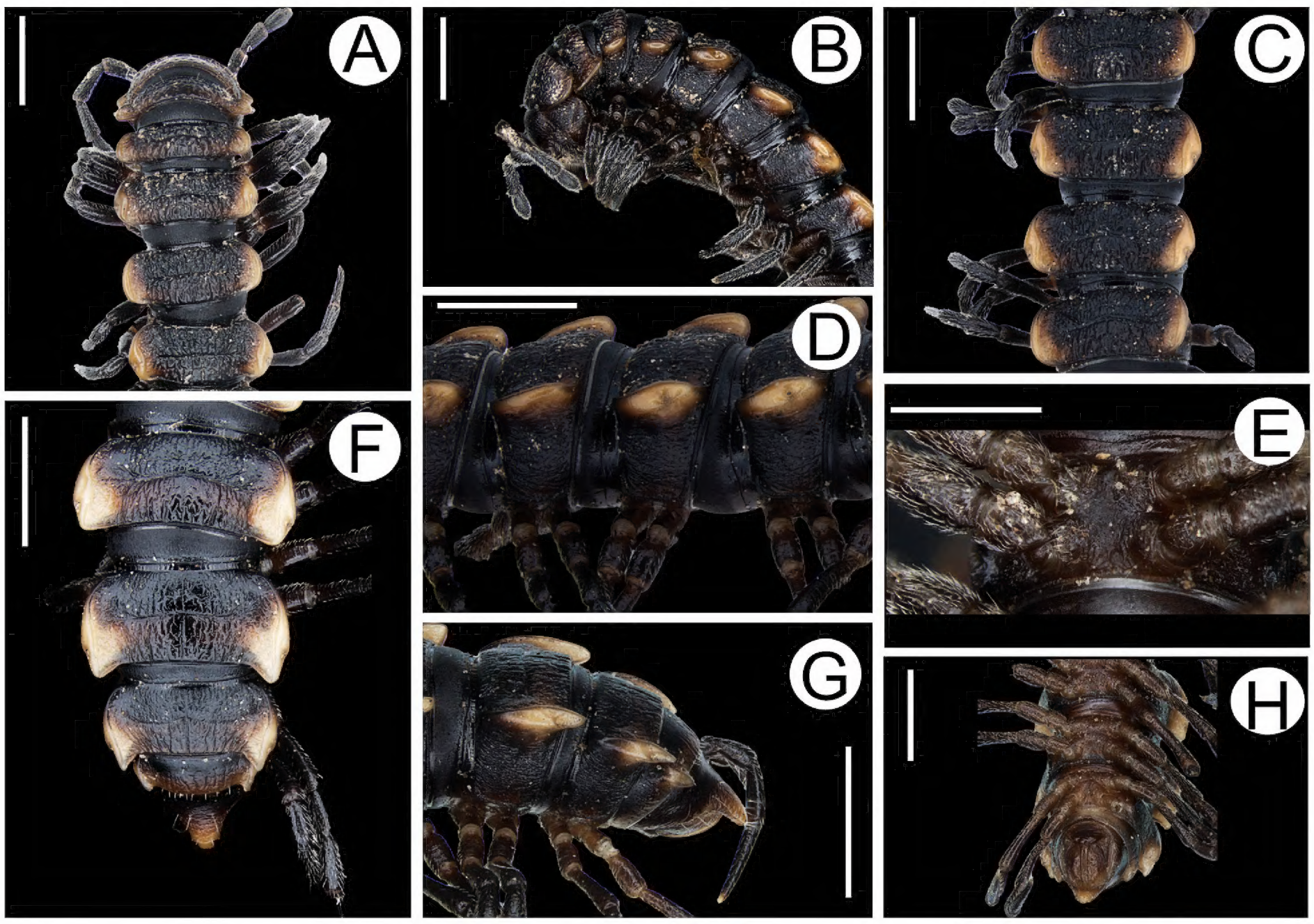

Figure 6. *Kronopolites corticinus* (Attems, 1936), comb. nov. **A.** Anterior part of body, dorsal view; **B.** Anterior part of body, lateral view; **C.** Segments 10 and 11, dorsal view; **D.** Segments 9–11, lateral view; **E.** Sternal cones between coxae 4, ventral view; **F–H.** Posterior part of body, dorsal, lateral, and ventral views, respectively. Scale bars: 2 mm (**A–D**, **F–H**); 1 mm (**E**).

Dajudeng, Yunnan (Golovatch 2020), and transferred to the genus *Mandarinopus* (Golovatch 2019). Similarly, *Kronopolites rugosus* Golovatch, 2013, described from Yuzhuqingtian, Yunnan, was also transferred to *Mandarinopus* by Golovatch (2019).

These two species are morphologically similar. Golovatch (2019) distinguished them based on the presence of a distofemoral process and a mesal process on the apical branch of the solenophore in *M. corticinus*, traits purportedly absent in *M. rugosus*. However, Golovatch

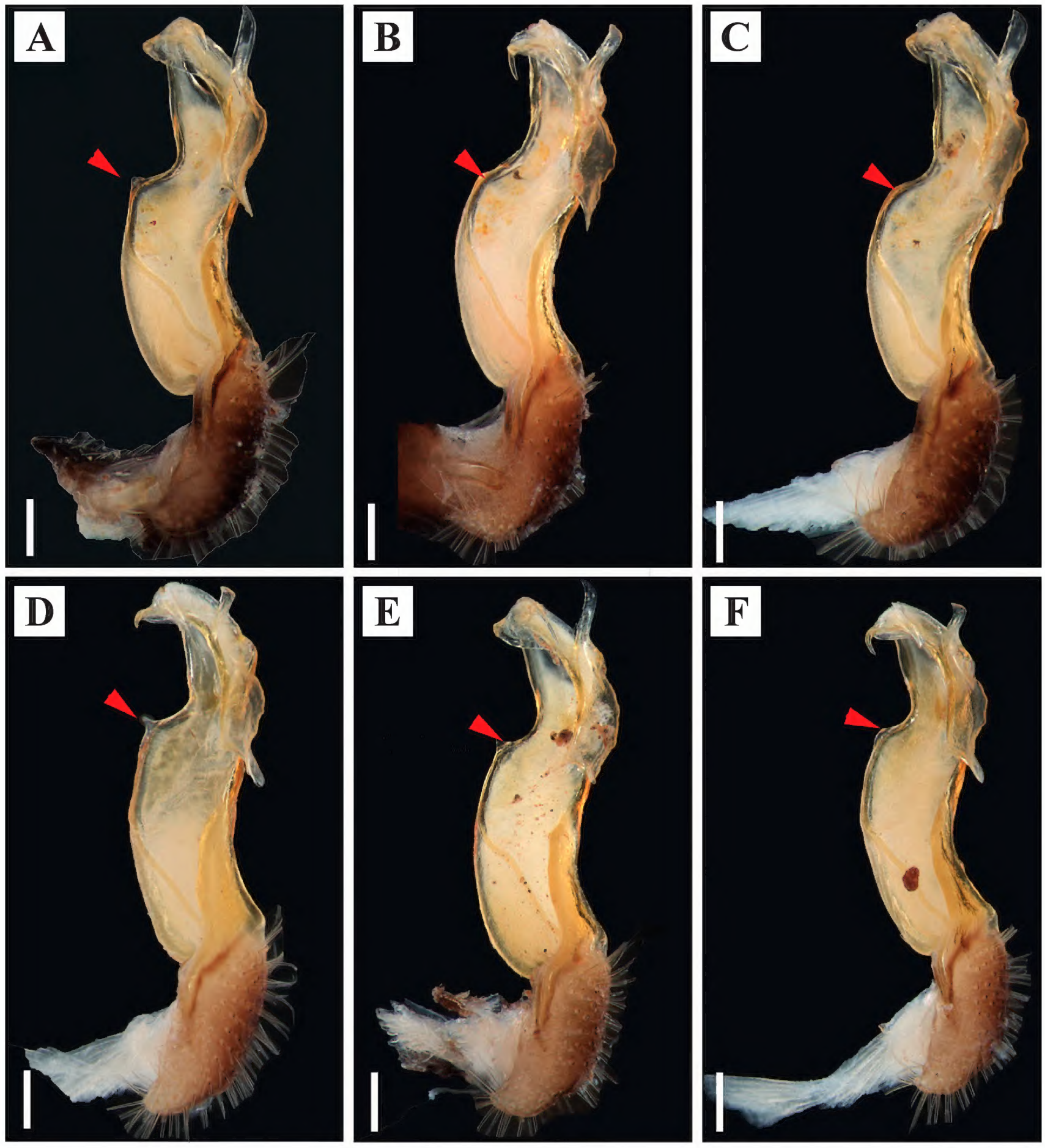

Figure 7. *Kronopolites corticinus* (Attems, 1936), comb. nov., left gonopod, ventral view. **A–C.** Collected from Dajudeng, Dali Bai Autonomous Prefecture, Yunnan; **D–F.** Collected from Yuzhuqingtian Scenic Area, Lijiang, Yunnan. Red arrows indicate the mesal process. Scale bars: 1 mm.

(2020) subsequently noted their striking resemblance and suggested that verification of their specific status would require additional material.

In the present study, we collected specimens morphologically similar to these taxa from their respective type localities, as well as from two additional sites. Morphological examination reveals that the diagnostic characters proposed by Golovatch (2019) are unreliable: the distofemoral process is not consistently present, even in specimens from the same population (Fig. 7), and the mesal process on the apical branch of the solenophore occurs in all examined specimens. Furthermore, genetic distance analysis based on COI sequences confirms that specimens from different localities are conspecific. Therefore, we formally propose *Kronopolites rugosus* as a junior synonym of *K. corticinus*.

Kronopolites semirugosus Golovatch, 2013, comb. restit.

Figs 8, 9

Kronopolites semirugosus Golovatch, 2013: 311–315, figs 35–44; Likhitrakarn et al. 2015: 32; Nguyen et al. 2025: 224.

Mandarinopus semirugosus: Golovatch 2019: 354; Golovatch and Liu 2020: 170.

Material examined. CHINA: Sichuan Province: 8 ♂♂ and 18 ♀♀ (CMMI 20240603001–20240603026), Liangshan Yi Autonomous Prefecture, Mianning County, Huian Town, Baixiluo (28.6412°N, 102.0908°E), asl. 2380 m, 3.VI.2024, Yifei Yu & Yuan Xiong leg.

Diagnosis. Differs from other species of the genus by the following combination of characters: collum and following metaterga rugose; sternal cones between ♂ coxae

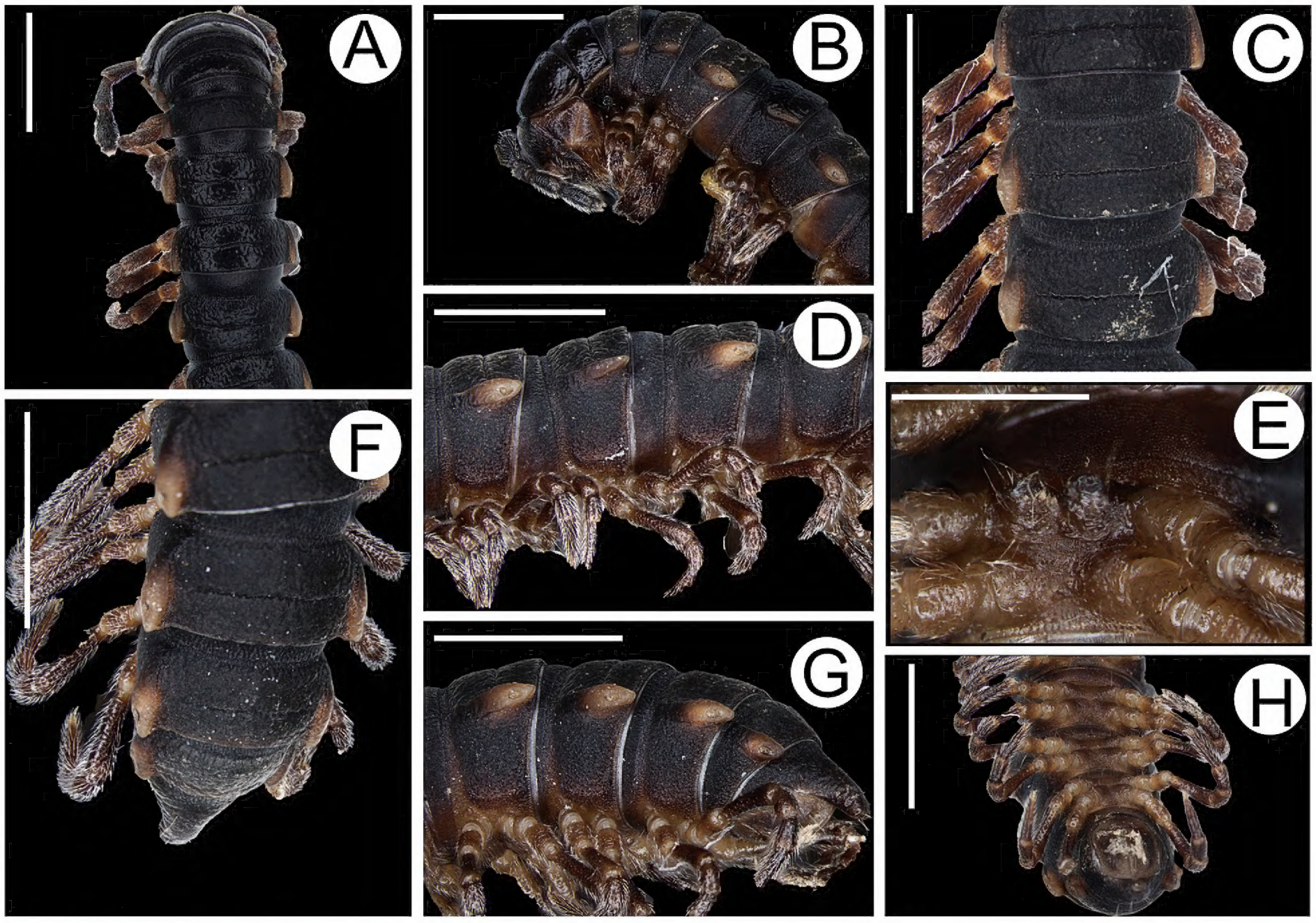

Figure 8. *Kronopolites semirugosus* (Golovatch, 2013), comb. restit. **A.** Anterior part of body, dorsal view; **B.** Anterior part of body, lateral view; **C.** Segments 10 and 11, dorsal view; **D.** Segments 9–11, lateral view; **E.** Sternal cones between coxae 4, ventral view; **F–H.** Posterior part of body, dorsal, lateral, and ventral views, respectively. Scale bars: 2 mm (**A–D**, **F–H**); 1 mm (**E**).

4 contiguous medially; gonopods without a distofemoral process, both larger processes of solenophore ribbon-shaped and rounded apically, subequal in shape and size (Golovatch 2019).

Distribution. China: Sichuan (Golovatch 2013b).

Remarks. Golovatch (2019) transferred this species from *Kronopolites* to *Mandarinopus*. Herein, we formally reject this transfer.

Kronopolites hirsutus (Golovatch, 2019), comb. nov.

Figs 3D, 10, 11

Mandarinopus hirsutus Golovatch, 2019: 350–354, figs 17–30; Golovatch and Liu 2020: 170.

Material examined. CHINA: Yunnan Province: 3 ♂♂ and 2 ♀♀ (20250803072–20250803076), Dali Bai Autonomous Prefecture, Jianchuan County, Laojunshan Town, Dajudeng (26.5891°N, 99.6094°E), asl. 2650 m, 3.VIII.2025, Xuankong Jiang, Yifei Yu & Yuan Xiong leg.

Diagnosis. Differs from other species of the genus by the following combination of characters: densely hirsute and rather uniformly black-brown to brown body, coupled with the absence of a distofemoral process on the gonopodal telopodite (Golovatch 2019).

Distribution. China: Yunnan (Golovatch 2019).

Remarks. This species is the only one in *Kronopolites* with a dense coat of setae on the body surface. Molecular evidence derived from newly collected topotypic material clearly demonstrates that this species is nested within the *Kronopolites* clade. This genetic confirmation effectively resolves the long-standing uncertainties triggered by its distinct external morphology (i.e., the hirsute metaterga), revealing that these somatic traits represent species-specific autapomorphies rather than diagnostic characteristics that justify generic-level differentiation.

Discussion

Phylogenetic relationships and generic synonymy

The primary objective of this study was to resolve the controversial delimitation between *Mandarinopus* and *Kronopolites*. Previous classifications relied heavily on gonopodal morphology, specifically the curvature and complexity of the solenomere and solenophore, to distinguish these genera. However, our molecular phylogenetic analyses (Figs 1, 2) clearly demonstrate that these morphological traits do not reflect evolutionary history.

The phylogenetic results reveal that *Mandarinopus* is polyphyletic and deeply embedded within the

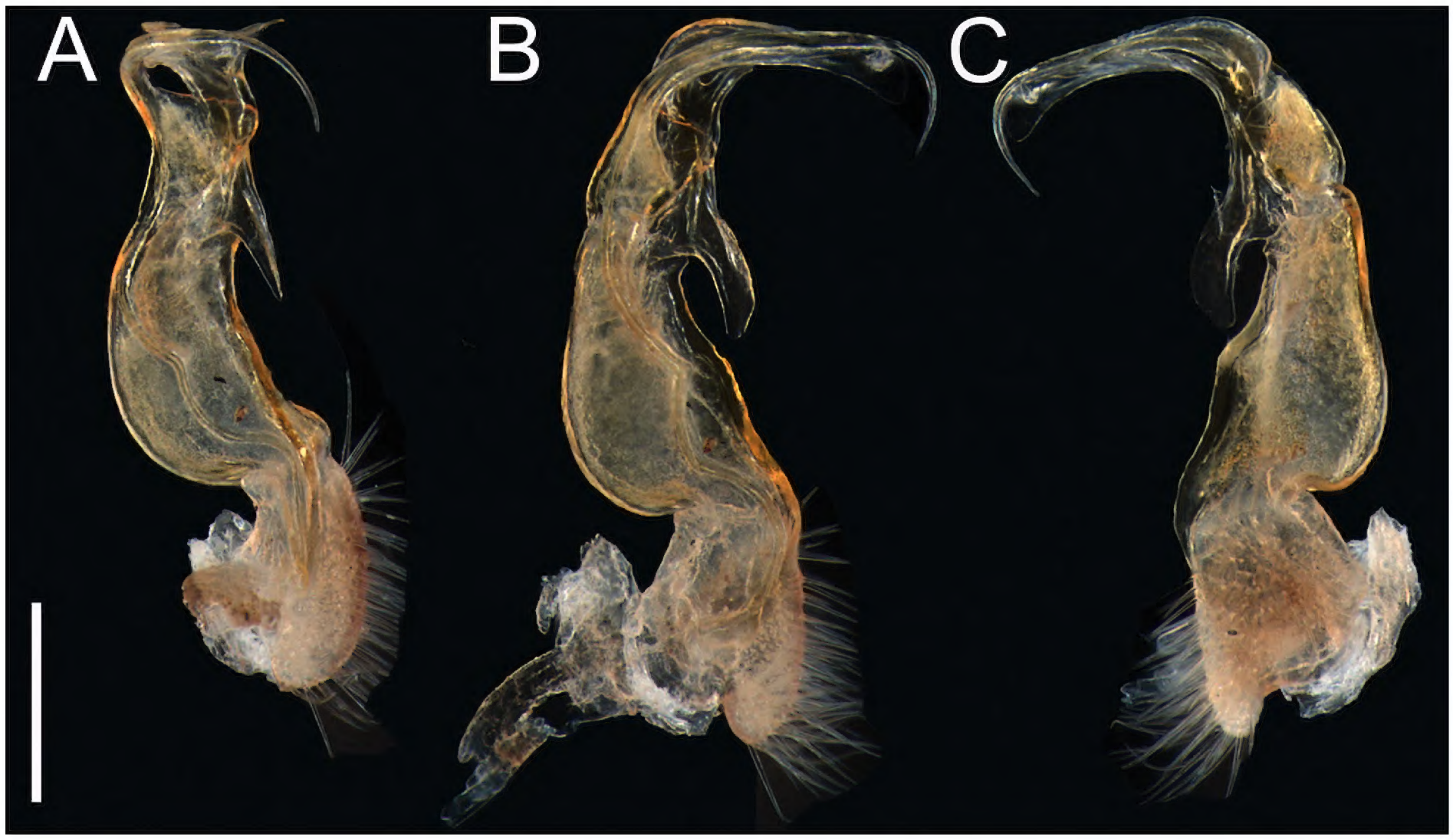

Figure 9. *Kronopolites semirugosus* (Golovatch, 2013), comb. restit., left gonopod. **A.** Ventral view; **B.** Mesal view; **C.** Lateral view. Scale bar: 2 mm.

Kronopolites clade. Critically, the type species of both genera, *Mandarinopus gracilipes* and *Kronopolites svenhedini*, are recovered as sister taxa with strong support (Clade B). This relationship renders *Kronopolites* paraphyletic if *Mandarinopus* is retained as a valid genus. Furthermore, the recovery of three distinct clades (A, B, and C) containing mixed species from both former genera indicates that the "*Mandarinopus*-type" gonopod morphology likely evolved independently or represents a plesiomorphic variation within the group. Consequently, the synonymy of *Mandarinopus* with *Kronopolites* is the only taxonomically stable solution.

Relationship with *Oxidus*

Jeekel (1968) previously hypothesized a close relationship between *Mandarinopus* and *Oxidus* based on gonopodal similarities. Our study explicitly refutes this hypothesis. Phylogenetically, the *Kronopolites* (including *Mandarinopus*) clade is distinct from the *Oxidus* clade (Figs 1, 2). This result is consistent with previous results by Nguyen (2017). Morphologically, *Oxidus* lacks the characteristic femoral fork (processes a and b) found in *Kronopolites*, further separating the two genera.

Morphological plasticity and specific synonymy

Our morphological examination corroborates the molecular data, highlighting the plasticity of characters previously considered diagnostic at the generic level. The distinction based on the "less curved" solenomere in *Mandarinopus* is invalid; for instance, the curvature in *K. semirugosus* comb. restit. is comparable to that of *Kronopolites ramosus*. Similarly, the distofemoral process (or "sharp thorn"), previously emphasized as a diagnostic feature for *K. gracilipes* comb. nov., proves to be an unstable character, appearing inconsistently even within species such as *K. corticinus* comb. nov.

At the species level, the validity of *K. rugosus* has been questioned because of its resemblance to *K. corticinus*. Our study confirms that the purported distinguishing features, namely the distofemoral process on the solenophore, are variable and overlap between the two nominal taxa. The distofemoral process is not consistently present in *K. corticinus* populations. Supported by our phylogenetic analysis, which recovers them as a monophyletic lineage with minimal genetic divergence, we formally propose *K. rugosus* comb. restit. as a junior synonym of *K. corticinus* comb. nov.

Meanwhile, given the extensive variation in somatic morphological traits, their application in higher-level taxonomy requires prudence and, ideally, corroboration by phylogenetic analyses. Somatic morphological traits (e.g., metatergal texture) historically prioritized as key diagnostic characters for generic classification are highly variable, evolutionarily labile, and prone to convergent evolution that results in homoplasy. A parallel pattern exists in the genus *Desmoxytes*, where striking variation in metatergal texture and analogous somatic features occurs even within a single monophyletic lineage. Widespread across unrelated clades, this trend underscores a critical conclusion: such somatic traits are products of evolutionary plasticity rather than conserved, genus-defining synapomorphies and therefore should not serve as the sole basis for establishing or retaining generic boundaries.

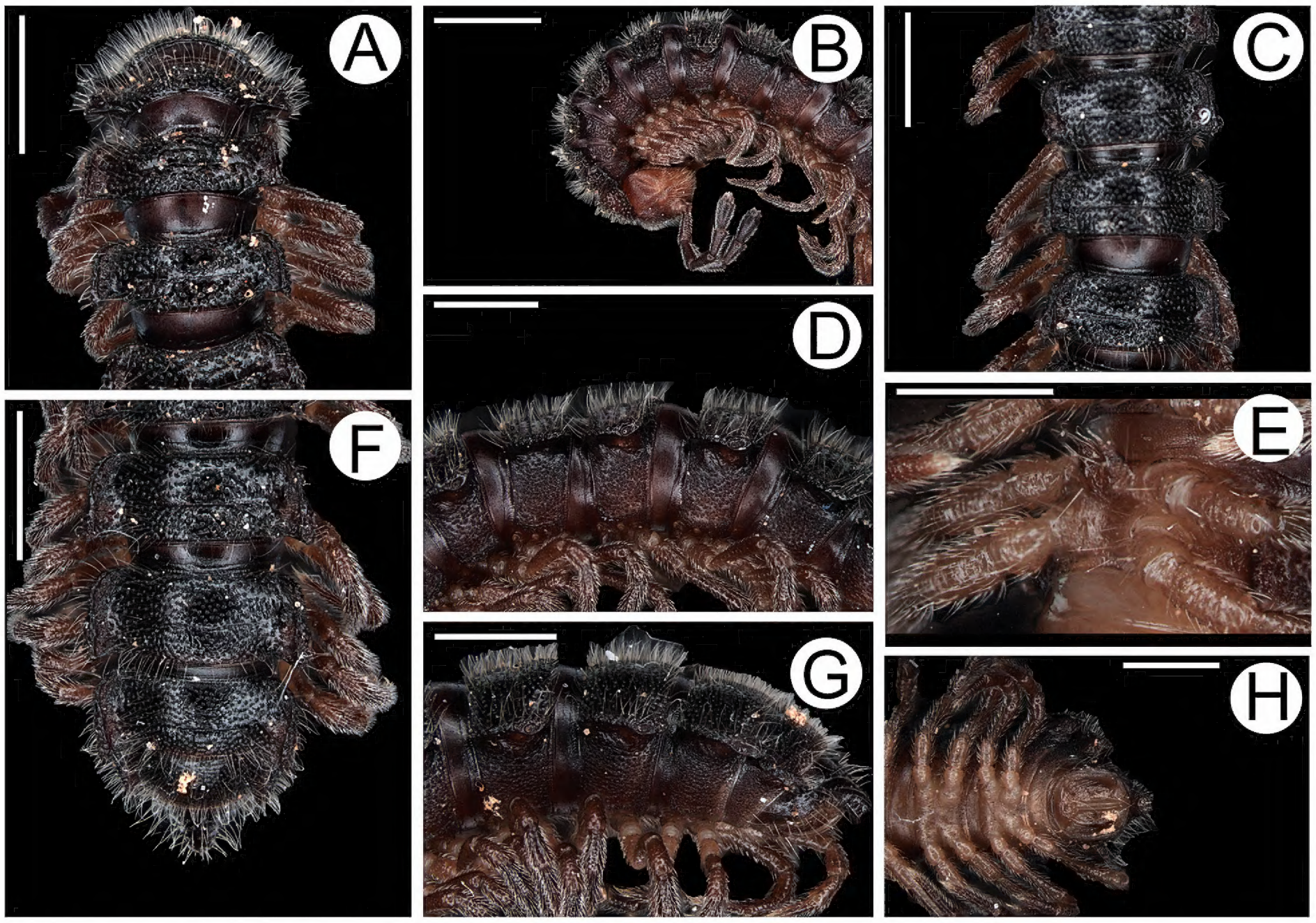

Figure 10. *Kronopolites hirsutus* (Golovatch, 2019), comb. nov. **A.** Anterior part of body, dorsal view; **B.** Anterior part of body, lateral view; **C.** Segments 10 and 11, dorsal view; **D.** Segments 9–11, lateral view; **E.** Sternal cones between coxae 4, ventral view; **F–H.** Posterior part of body, dorsal, lateral, and ventral views, respectively. Scale bars: 5 mm.

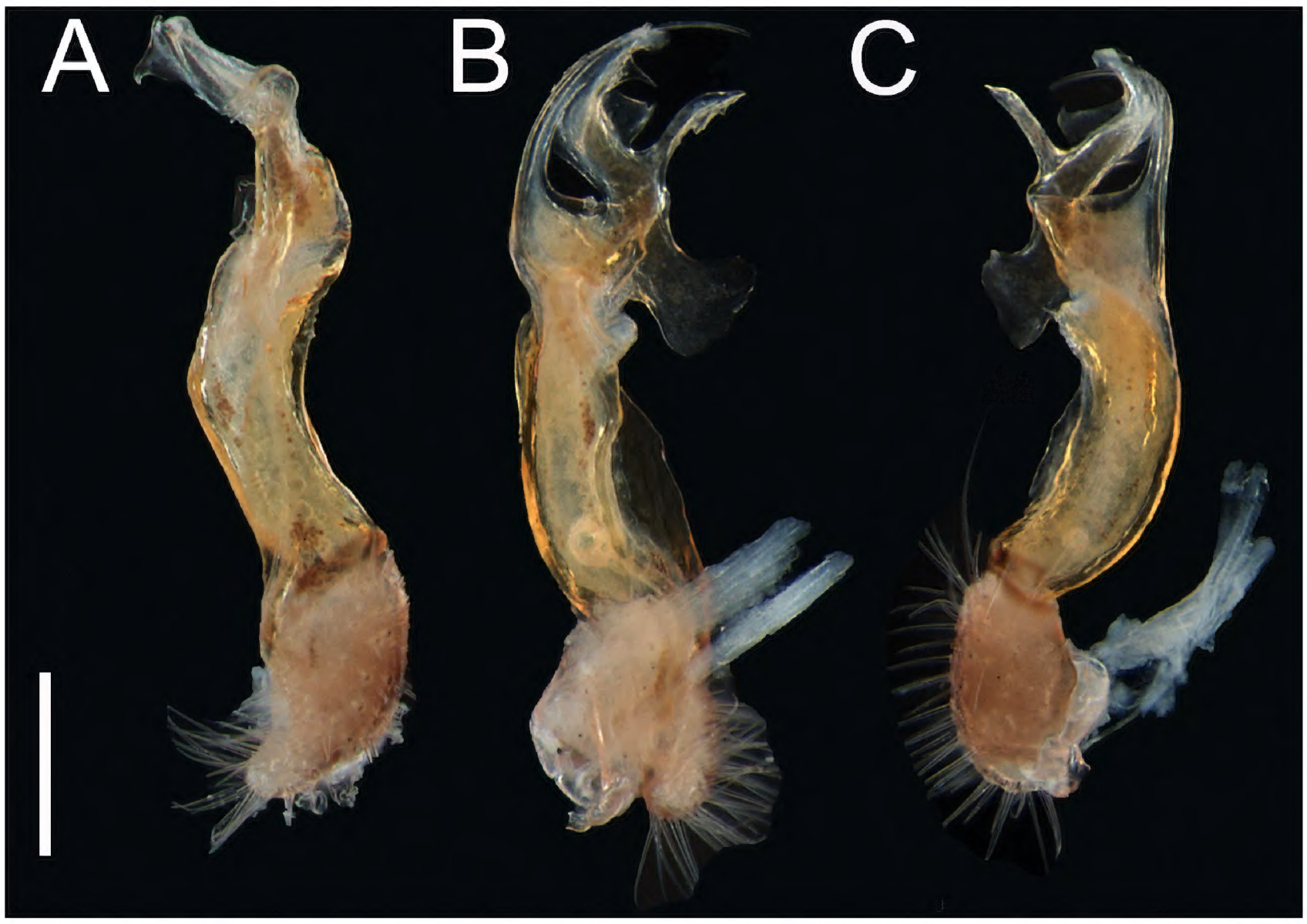

Figure 11. *Kronopolites hirsutus* (Golovatch, 2019), comb. nov., left gonopod. **A.** Ventral view; **B.** Mesal view; **C.** Lateral view. Scale bar: 2 mm.

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Supplementary material 1

Species vouchers and accession numbers

Authors: Yuan Xiong, Huiming Chen, Luqi Huang, Xuankong Jiang, Chao Jiang

Data type: xlsx

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